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Differences in Englemann Spruce Forest Biogeochemistry East and West of the Continental Divide in Colorado, USA

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Abstract

We compared Englemann spruce biogeochemical processes in forest stands east and west of the Continental Divide in the Colorado Front Range. The divide forms a natural barrier for air pollutants such that nitrogen (N) emissions from the agricultural and urban areas of the South Platte River Basin are transported via upslope winds to high elevations on the east side but rarely cross over to the west side. Because there are far fewer emissions sources to the west, atmospheric N deposition is 1–2 kg N ha^{-1} y^{-1} on the west side, as compared with 3–5 kg N ha^{-1} y^{-1} on the east side. Species composition, elevation, aspect, parent material, site history, and climate were matched as closely as possible across six east and six west side old-growth forest stands. Higher N deposition sites had significantly lower organic horizon C:N and lignin:N ratios, lower foliar C:N ratios, as well as greater %N, higher N:Ca, N:Mg, and N:P ratios, and higher potential net mineralization rates. When C:N ratios dropped below 29, as they did in east-side organic horizon soils, mineralization rates increased linearly. Our results are comparable to those from studies of the northeastern United States and Europe that have found changes in forest biogeochemistry in response to N deposition inputs between 3 and 60 kg ha^{-1} y^{-1}. Though they are low by comparison with more densely populated and agricultural regions, current levels of N deposition, have caused measurable changes in Englemann spruce forest biogeochemistry east of the Continental Divide in Colorado.

Key words: nitrogen deposition; nitrogen cycling; foliar chemistry; nitrogen mineralization; forest ecosystems; Colorado.

Introduction

Due to the proximity of urban and agricultural emission sources, atmospheric nitrogen (N) inputs are higher east of the north-central Colorado Continental Divide than they are to the west (Parrish and others 1990; Langford and Fehsenfeld 1992). A majority of Colorado's population of 4 million resides on the east side of the Continental Divide, and the region is also important in terms of agriculture and livestock production (Baron and others 2000b). The greatest concentration of nitrogen oxide (NO_x) emissions from point and mobile sources is found in Front Range metropolitan areas (Williams and Tonnessen 2000). Local easterly winds transport some of this N to high-elevation watersheds east of the Continental Divide (Parrish and others 1986, 1990; Sievering and others 1989; Langford and Fehsenfeld 1992). The combination of anthropogenetic N sources and orographic precipitation results in higher N deposition at high-elevation sites (Williams and Tonnessen 2000). Strong westerly winds in the upper atmosphere prevent these N-enriched air masses from crossing the Continental Divide

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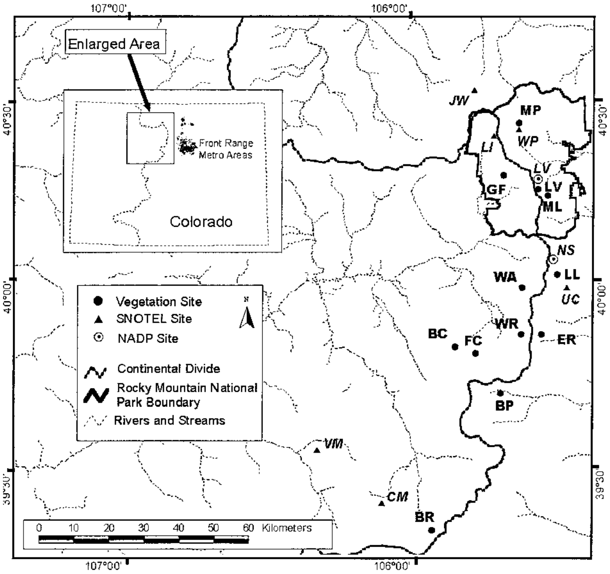

Figure 1. Location of forest, SNOTEL, and NADP sites. For SNOTEL site abbreviations, see Table 1.

(Bossert 1990; Baron and Denning 1993). Two recent reports of NO_3^- and NH_4^+ concentrations from the monitoring stations of the Colorado National Atmospheric Deposition Program/National Trends Network (NADP/NTN) showed that sites east of the Continental Divide had significantly greater concentrations of NO_3^- and NH_4^+ than western sites (Baron and others 2000b; Heuer and others 2000).

NADP/NTN monitoring stations east of the Continental Divide have documented mean annual wet inorganic N deposition of 3.6 kg ha^{-1} y^{-1} for Niwot Saddle (NS) for the period from 1984 to 1998 and 3.5 kg ha^{-1} y^{-1} for Loch Vale (LV) for 1985–98 (Figure 1) (Williams and others 1998; NADP/NTN 1999). These sites thus have the highest N deposition rates in Colorado. Total (wet + dry) N deposition to Niwot Saddle and Loch Vale was respectively estimated at 3.0–5.0 kg ha^{-1} y^{-1} (for 1993–94) and 3.2–5.5 kg ha^{-1} y^{-1} (for 1992–97) (Sievering and others 1996; Campbell and others 2000). Reported wet inorganic N deposition at Fraser Experimental Forest, a west-side site, averaged 1.7 kg ha^{-1} y^{-1} for 1984–86 and 1.1 kg ha^{-1} in 1990 (Stottlemyer and Troendle 1992; Stottlemyer and others 1997). Other west-side NADP/NTN stations have recorded wet N deposition values that range from 1.1 to 1.7 kg ha^{-1} y^{-1} for the period from 1988 to 1997. Dry deposition estimates are unavailable for west-side sites. We do not expect dry deposition at the west sites to alter the pattern of higher deposition rates at the east-side sites.

Lake chemistry data and paleolimnological research indicate that high-elevation aquatic systems east of the Continental Divide have been affected by N deposition (Baron and others 2000b; Williams and Tonnessen 2000). Therefore, we designed a study to explore whether there were significant changes in Englemann spruce (*Picea englemannii*) forests caused by N deposition. Other researchers have already documented measurable changes in forest biogeochemical parameters in regions that receive elevated N deposition (Vitousek and others 1997; Aber and others 1998; Fenn and others 1998; Gundersen and others 1998). However, comparison studies have demonstrated that there are gradients in the responses across regions of increasing N deposition (McNulty and others 1991; Tietema and Beier 1995; Aber and others 1998; Gundersen and others 1998; Lovett and Rueth 1999). In Colorado, where N deposition ranges from 1.0 to 5.0 kg ha^{-1} y^{-1}, we postulated that differences in N-cycling parameters would be detectable in high-elevation old-growth forests because of low N demand.

Materials and Methods

Climate

To characterize the climate conditions of north-central Colorado, we compared data from six high-elevation National Resources Conservation Service SNOTEL sites (SNOwpack TELemetry) and two meteorological stations within the study area (National Resources Conservation Service 1999) (Figure 1 and Table 1). Because most (65%–80%) annual precipitation at these sites occurs as snow, annual precipitation was divided into two seasons, summer (June–September) and winter (October–May), based on whether a majority of the precipitation occurs as rain or snow (Baron and Denning 1993; Stottlemyer and others 1997). We then compared the climate at the east and west sites by season to determine whether there were differences in the precipitation regime that could influence forest processes.

Study Sites

Twelve old-growth closed-canopy Englemann spruce (*Picea englemannii*) sites were sampled in August and September 1998 and again in August 1999. Old-growth stands were chosen to obviate the effects of land-use history. Site selection was based on US Forest Service old-growth maps, personal communication with T. T. Veblen of the University of Colorado, a 30-m–resolution land cover type and stand density map of Rocky Mountain National Park, and considerations of accessibility.

Table 1. Climate Characterization of Two Meteorological Stations and Six SNOTEL Sites

Site Name (Abbreviation)	Elevation (m)	Side[a]	Annual Mean Precip. (cm)	Winter Precip. Oct.–May (cm)	Summer Precip. June–Sept. (cm)	Period of Record[c]	Mean Jan. Temp. (°C)	Mean July Temp. (°C)	Mean Annual Temp. (°C)
Joe Wright (JW)[b]	3217	E	117	87	30	1989–99	−8.4 (2.9)	11.6 (5.2)	0.02 (1.7)
University Camp (UC)[b]	3140	E	89	65	24	1990–99	−8.3 (0.8)	10.8 (0.9)	0.2 (0.5)
Willow Park (WP)[b]	3262	E	99	75	24	1989–99	−10.0 (0.9)	9.2 (0.8)	−1.1 (0.5)
Loch Vale (LV)[d]	3160	E	112 (17)	82 (13)	30 (8)	1992–99	−7.8 (0.8)	12.3 (0.9)	1.1 (0.6)
Copper Mt. (CM)[b]	3201	W	81	61	20	1986–99	−11.0 (3.7)	9.9 (1.3)	−0.4 (2.1)
Lake Irene (LI)[b]	3262	W	91	70	21	1985–99	−10.6 (3.1)	9.0 (2.7)	−1.4 (0.7)
Vail Mt. (VM)[b]	3140	W	87	69	18	1986–99	−8.9 (1.4)	12.5 (1.3)	1.2 (0.5)
Fraser (FC)[e]	3189	W	86 (16)	62 (15)	24 (4)	1984–93	−10.7 (1.7)	13.8 (1.4)	0.8 (0.9)
East Side Average	—	—	104	78	26	—	−8.6	11.0	0.06
West Side Average	—	—	86	65	21	—	−10.3	11.3	0.1
P Value	—	—	0.11	0.25	0.86	—	0.99	0.42	0.67

Mean and one standard deviation (SD) are given in parentheses. Standard deviations were not provided by the NRCS for the SNOTEL precipitation data.
[a]*Side indicates either east (E) or west (W) of the Continental Divide.*
[b]*Precipitation data 1961–90 for SNOTEL sites*
[c]*Period indicates years used for mean temperatures.*
[d]*J. S. Baron unpublished; precipitation data 1985–98*
[e]*M. Ryan unpublished; precipitation data 1992–99*

All stands were dominated by Englemann spruce and had a *Vaccinium spp.* understory. Other overstory species included subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*). These were mesic spruce–fir forests characterized as cool, sheltered, and well-drained, with relatively deep soils (Peet 1981). Sites were northeast-facing at an elevation of 3000–3500 m; the slope angle averaged 10°–20°. The bedrock of all stands consisted of Precambrian granite, schist, and gneiss (Lovering and Goddard 1950). The soils were shallow and coarse-textured, with an overlying organic layer averaging 5 cm deep. Each site consisted of three 30 × 30 m plots within a 0.5-km radius. Six sites were located east of the Continental Divide and six sites were west of it (Figure 1). The entire study area was 110 × 50 km.

To determine species basal area, diameter at breast height (dbh; 1.3 m) and species were recorded for each live tree greater than 5 cm dbh. Basal area data and tree cores were collected at all sites except Granite Falls (GF), due to site accessibility constraints. Tree cores were initially collected to estimate stand age to support our old-growth classification. Growth rates were subsequently determined to establish whether slight changes in climate could have influenced production. Nine cores per site were collected using an increment borer at breast height (1.3 m) from three canopy spruce trees in each plot. Collection continued until three complete cores were obtained in which the pith was intercepted and rotten sections were absent. The cores were processed following standard dendrochronological methods (Stokes and Smiley 1968; Phipps 1985). They were stored in paper straws until processed, then glued to wooden mounts and sanded. Rings were counted and measured under a dissecting microscope to the nearest 0.25 mm to determine tree age at coring height and growth rates. Because the outside date of all samples was known and only complete cores were analyzed, cross-dating was obtained visually. The average growth rate was determined for two 30-year periods: 1900–29 and 1930–59. These time periods were chosen to compare growth rates during different regional climatic regimes (Veblen and others 2000). The years 1900–29 and 1930–59 were characterized as cool–wet and warm–dry, respectively. Trees less than 100 years old in 1900 were removed from the statistical analysis of growth rates because younger trees with higher growth rates could confound comparisons.

Foliar Sampling and Analysis

Current-year foliage was sampled from five canopy trees in each plot at 11 of the 12 sites (15 samples per site; East Rollins [ER] was not sampled due to inaccessibility of current-year foliage in the lower canopy). Sampling was done in August and September because the full expansion of current-year needles concludes in July and the end of the growing season represents stable nutrient concentrations (Fernandez and others 1990). Lower canopy branches (height: 10 m) from the tree aspect judged to receive the greatest sunlight were collected using a tree trimmer, stored in plastic bags, and refrigerated until processed. Needles were rinsed with deionized water to remove particles and contamination and then dried at 25°C. Needles were removed from the branch and a subsample was ground to fine powder.

Percent carbon (C) and N were measured using a dry combustion autoanalyzer (CHN-1000; LECO Corporation, St. Joseph, MI, USA). Samples were digested using nitric and perchloric acids and analyzed by inductively coupled plasma (ICP) (model 61E; Thermo-Jarrell Ash, Franklin, MA, USA) for calcium (Ca), magnesium (Mg), phosphorus (P), and potassium (K) (Self and Rodriguez 1998).

Vector analysis was used to interpret differences in foliar nutrient concentrations between east and west sites (Timmer and Stone 1978; Haase and Rose 1995; Kiefer and Fenn 1997). Vector analysis is a method used to assess plant nutrient status and plant nutrient response to treatments such as fertilization. Needle weight often increases with fertilization, which confounds interpretations of changes in nutrient content or concentration. Vector analysis allows simultaneous comparisons of nutrient concentration (percent dry weight) and content (μg needle^{-1}) and a unit of plant weight in a graphical format. The result is an index of nutrient dilution, sufficiency, deficiency, or luxury consumption relative to a subjectively identified standard.

Nutrient and weight values were normalized to a reference point that has a value of 100 for all three parameters (weight, concentration, and content). Vectors were drawn from the reference point to other points that represent relative changes in nutrient status and weight. The magnitude and direction of the line represents the combined response. Shifts along the diagonal 1:1 line represent no change in unit plant weight; shifts to the right or left indicate an increase or decrease in unit plant weight, respectively. Horizontal shifts represent changes in content and not concentration, and shifts along the vertical represent changes in concentration and not content.

The reference point was the average of all west-side foliar chemistry and was used to examine changes in nutrient status with elevated N inputs. The unit of plant weight used in all cases was average needle dry weight. To determine average east- and west-site needle weight, five samples were randomly chosen from each site and 100 needles were weighed.

Soil Sampling and Analysis

In 1998, five organic horizon and five mineral horizon (to a depth of 20 cm) soil samples were collected at each plot (15 samples per site). Organic horizon samples consisted of four or five adjacent 6.6-cm–diameter cores so that enough sample would be available for analysis. One core was taken to a depth of 20 cm to obtain a mineral horizon sample. Samples were packed in ice during transport to the laboratory and then stored at 4°C. Organic horizon samples were homogenized through an 8-mm sieve to remove large roots and rocks, and total sample weight was recorded. A subsample was dried at 25°C and ground. The negative one-third bar water potential method was used to measure field capacity (Klute 1986). Mineral horizon samples were dried at 25°C; the dried samples were then sieved through a 2-mm sieve and a subsample was ground. Percent C and N were assessed on ground mineral and organic horizon samples. We measured organic horizon percent lignin with the Van Soest fiber method (Goering and Van Soest 1970). Organic horizon mass per unit area was determined using total sample dry weight and area sampled. The organic horizon N pool was calculated using %N and mass per unit area data.

Yearly leaching losses of NO_3^- and NH_4^+ were estimated using soil ion exchange resin bags (Binkley and Hart 1989). The resin bags consisted of 10 g each of anion and cation exchange resin in a nylon stocking. Ten bags per plot were placed below the organic soil horizon in 1998 and collected 1 year later. Resin bags were extracted with 100 ml 2 M KCl-PMA and analyzed for NO_3^- and NH_4^+ using an Alpkem autoanalyzer (3500 series; Alpkem Corporation, Perstorp Analytical Company, Wilsonville, OR, USA).

Potential organic horizon net mineralization and nitrification rates were estimated with a laboratory soil incubation using methods modified from Binkley and Hart (1989). A moist subsample was brought to field capacity using deionized water. A plastic specimen cup containing 35 g of soil was placed in a 1-L mason jar with 30 ml of deionized water to maintain humidity. Another 15-g moist subsample was extracted with 75 ml 2 M KCl-PMA. Soils were incubated in the dark at 20°C for 35 days. We opened the jars once a week to reduce carbon dioxide (CO_2) buildup, and deionized water was added to samples to maintain field capacity. After 5 weeks, a 15-g subsample was extracted with 75 ml 2 M KCl-PMA. An Alpkem autoanalyzer was used to analyze KCl extracts for NO_3^- and NH_4^+. Mineralization and nitrification rates were calculated by the difference in NO_3^- plus NH_4^+ and NO_3^-, respectively, between the incubated and initial extracts.

General soil characterization measurements included soil texture, pH, organic matter fraction, and mineral soil extractable cations. The hydrometer method was used to assess soil texture on sieved mineral horizon samples (Klute 1986). A 1:5 soil-to–deionized water ratio was used to determine organic and mineral horizon pH; this ratio was necessary to provide enough liquid headspace for measurement. The soil–water mixer was shaken for 10 min and then allowed to settle for 20 min before measurement. The loss-on-ignition method was used to measure organic matter fraction on dry organic and mineral horizon subsamples. Samples were baked at 500°C for 6 h, and organic matter content was calculated by difference. Extractable mineral soil cations and P were estimated using ammonium acetate and analyzed by ICP (Page 1982).

Statistical Calculations

Differences between east and west foliar and soil analyses were tested using an analysis of variance, two-stage nested, mixed-effect model (SAS 1989). East versus west was considered a fixed effect because side was not randomly selected. Site was a random effect nested within side. Plot was a random effect nested within site and side. General linear model analysis was performed to determine the relationship between mineral soil organic matter fraction with clay content and %N. Statistical differences between east and west climate characteristics were determined with a *t*-test. Differences were considered significant at a level of $P < 0.05$ unless otherwise stated.

Results

Climate

No statistical differences were found between east and west climatic variables (Table 1). Both east and west forest stands are cold, with mean annual temperatures of 0.06°C and 0.1°C, respectively. The west sites were slightly drier and received about 18 cm less precipitation per year than the east sites (Table 1). Annual mean precipitation was 104 cm (range, 89–117) in the east and 86 cm (range, 81–91) in the west. We postulated that differences in precipitation during the summer months would have a greater biogeochemical impact than differences during the winter. A total of 13 cm of the 18-cm mean difference in precipitation between the east and west sites occurred in the winter and may have affected snowpack depth during spring; the other 5 cm occurred during the snow-free season (Table 1).

Stand Characteristics

There were no significant differences between stand age and spruce or fir basal area between the east and west sites (Table 2). The average age of dominant spruce trees was 328 years (range, 113–506) for east sites and 294 years (range, 150–552) for west sites (Table 2). Total basal area averaged 58 and 52 $m^2\ ha^{-1}$, respectively, for the east and west sites. This supports our classification of the forests as mesic Englemann spruce because xeric stands would have lower total basal area values (30–40 $m^2\ ha^{-1}$) (Peet 1981). Spruce and fir basal area averaged 39 and 19 $m^2\ ha^{-1}$ and 35 and 14 $m^2\ ha^{-1}$ for the east and west sites, respectively. Lodgepole pine occurred at four west sites (Boreas Pass [BR], Fool Creek [FC], West Arapaho [WA], and West Rollins [WR]) and represented from 4% to 22% of the total basal area at each site. Growth rates were comparable between the east and west sites for the two time periods that we analyzed, suggesting that high-elevation spruce stands were insensitive to the relative drought of 1930–59 and the relatively wet period of 1900–29 (Table 2).

Foliar Analyses

There was little variation in foliar chemical characteristics among the east and west samples (see stand deviations in Table 3). The mean values for all east sites showed significantly higher foliar %N and lower C:N ratios than the west sites (Table 3). Foliar N:Ca, N:Mg, and N:P ratios were significantly higher at the east sites than the west sites, although foliar %Ca, %Mg, %K, and %P did not differ between the east and west sites.

The average nutrient concentration and content and needle weight of all west-side foliage was used as the reference point for vector analysis (Figure 2). Because east-side needles weighed an average of 17% more, relative unit dry weight increased to

Table 2. Summary of Forest Stand Characteristics by Site

Site	Side	Stand Age (y)	Total Basal Area (m^2 ha^{-1})	Spruce Basal Area (m^2 ha^{-1})	Growth Rate 1900–29 (mm y^{-1})	Growth Rate 1930–59 (mm y^{-1})
Boreas Pass (BR)	W	255 (36)	44 (6)	38 (8)	0.39 (0.24)	0.37 (0.17)
Fool Creek (FC)	W	250 (29)	58 (13)	35 (20)	0.29 (0.06)	0.25 (0.06)
Byers Creek (BC)	W	401 (153)	65 (9)	41 (9)	0.43 (0.39)	0.47 (0.46)
West Rollins (WR)	W	213 (63)	40 (9)	29 (7)	0.57 (0.12)	0.59 (0.37)
West Arapaho (WA)	W	358 (100)	51 (9)	31 (11)	0.50 (0.26)	0.58 (0.38)
Long Lake (LL)	E	422 (42)	80 (21)	60 (28)	0.29 (0.11)	0.33 (0.14)
East Rollins (ER)	E	238 (25)	65 (9)	44 (6)	0.38 (0.14)	0.41 (0.18)
Berthoud Pass (BP)	E	294 (44)	47 (12)	32 (11)	0.55 (0.29)	0.47 (0.21)
Loch Vale (LV)	E	350 (101)	50 (11)	29 (6)	0.49 (0.27)	0.46 (0.26)
Marmot Point (MP)	E	313 (109)	61 (1)	39 (3)	0.65 (0.28)	0.58 (0.24)
Mills Lake (ML)	E	349 (133)	43 (1)	29 (6)	0.53 (0.34)	0.46 (0.21)
East Side Average	—	328 (100)	58 (16)	39 (16)	0.47 (0.26)	0.45 (0.21)
West Side Average	—	294 (111)	52 (12)	35 (11)	0.42 (0.25)	0.44 (0.32)
P Value	—	0.52	0.43	0.51	0.47	0.91

Mean and one standard deviation (SD) are given in parentheses.
Side indicates either east (E) or west (W) of the Continental Divide.
Stand age is the age of canopy spruce trees at coring height (1.3 m).
Granite Falls data was not available due to inaccessibility.
Sample n = 9 per site for stand age and growth rate data.
Degrees of freedom are nine for all analyses.

Table 3. Summary of Foliar Chemistry of Current Year Englemann Spruce Needles

Analysis	East Average	East Range	West Average	West Range	*P* Value
N (%)	1.14 (0.1)	0.91–1.44	0.99 (0.1)	0.73–1.32	0.02
C:N	45.6 (4.2)	36.3–55.8	52.1 (6.6)	37.7–68.9	0.03
Ca (%)	0.31 (0.08)	0.18–0.51	0.35 (0.09)	0.14–0.63	0.26
Mg (%)	0.097 (0.01)	0.07–0.13	0.10 (0.01)	0.08–0.14	0.09
K (%)	1.34 (0.3)	0.79–2.03	1.19 (0.3)	0.74–2.11	0.42
P (%)	0.19 (0.04)	0.12–0.28	0.21 (0.03)	0.16–0.36	0.16
N:Ca	3.83 (0.9)	2.17–6.41	2.99 (0.8)	1.59–6.13	0.007
N:Mg	11.9 (1.7)	8.78–16.6	9.66 (1.6)	6.78–14.4	0.003
N:P	6.34 (1.3)	4.39–9.99	4.77 (0.7)	3.00–7.47	0.008

Mean and one standard deviation (SD) are given in parentheses; range is minimum and maximum values.
Nitrogen and nutrients are percentages of oven-dry weight.
Sample n = 75 and 90 for all analyses for east and west sites, respectively.
Degrees of freedom are nine for all analyses.

117. The decrease in Ca and P concentration and relatively unchanged nutrient content represents a dilution effect due to increased east-side needle weight not being compensated by greater uptake. There was little dilution effect for Mg because content compensated for increased needle weight; therefore, we saw less of a decrease in concentration. The large increase in N and K content and slight increase in concentration indicate that N and K are available in sufficient quantities to more than compensate for increased needle weight at east sites and that N is less limiting in east forests than in west ones. The substantial increase in N:Mg, N:Ca, and N:P content at east compared to west sites indicates that the ratio of μg N to μg Mg, Ca, or P per needle has increased.

Soil Analyses

As with foliar chemistry, mineral horizon results were similar enough across all east and west sites

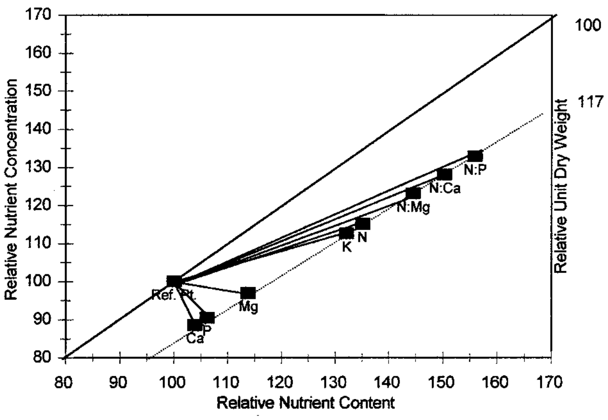

Figure 2. Foliar vector analysis comparing average west to east side foliar nutrient status and illustrating the relationship between current-year nutrient concentration and content and needle dry weight. The 1:1 line represents no changes in relative unit dry weight; the dotted line represents a relative increase of 17% (or 117). The reference point (Ref. Pt.) refers to west-side foliar nutrient status. For each nutrient, west-side foliar nutrient status was normalized to 100 for all three parameters. Vectors from the reference point represent relative changes in nutrient status and weight of east-side as compared to west-side foliage.

that only summary data are presented (Table 4). Organic and mineral horizon pH and organic matter fraction did not differ between east and west sites (Table 4). Organic horizon pH averaged 4.99 (range, 4.20–5.72) and 5.28 (range, 4.25–6.85) for the east and west sites, respectively, and mean organic matter fraction was 0.65 (range, 0.39–0.81) for the east sites and 0.62 (range, 0.33–0.83) for the west sites. Mineral horizon percent sand and silt were similar for the east and west sites (Table 4). Percent clay was greater at the east than at west sites; the average difference was 4.9%. No significant differences were observed in mineral soil extractable Ca, Mg, K, sodium (Na), and P.

East-side mineral horizon soils had marginally greater %N ($P = 0.08$), but there was no difference between the east and west sites in %C (Table 4). Mineral horizon C:N ratios were significantly lower at east sites than at west sites. Significant relationships were found between mineral soil clay content and organic matter fraction ($P < 0.0001$, $R^2 = 18\%$) as well as between mineral soil organic matter fraction and %N ($P < 0.0001$, $R^2 = 83\%$).

Organic horizon mass per unit area did not differ between the two sides, and the organic horizon N pool was significantly greater at east sites (Table 5). East sites had significantly greater organic horizon %N. Organic horizon %C did not differ between east and west sites. Organic horizon C:N ratios were thus significantly lower at east sites than at west sites. Organic horizon %lignin was not significantly different between east and west sites; however, lignin:N ratios were significantly lower at east sites than at west sites because of differences in %N.

Potential net mineralization rates were significantly greater at east sites than at west ones (Table 5). Potential net nitrification rates were low at all but two sites (Loch Vale [LV] and Mills Lake [ML]) and did not differ between east and west sites. Although estimated leaching losses of NO_3^- and NH_4^+ from resin bags were greater at east than at west sites, the differences were not significant. Two east sites (again, LV and ML) had the highest average NO_3^- losses (1.4 and 3.1 mg N y^{-1}, respectively). The range was 0–60 mg N y^{-1} for east sites and 0–0.7 mg N y^{-1} for west sites. The relationship between organic horizon %N and potential net mineralization rate shows a threshold of 1.2% N, above which mineralization increases linearly (Figure 3A). At the west sites, %N was less than 1.4 and mineralization rates were low; east sites had at least 1.3% N and higher mineralization rates. Similarly, when C:N ratios were 29 or lower, mineralization rates increased linearly (Figure 3B). West sites had C:N ratios greater than 29 and low mineralization rates; east sites had C:N ratios less than 29 and higher mineralization rates.

We asked whether differences in wet N deposition inputs could account for the observed differences in organic horizon N pools between the east and west sites. Using the mean organic horizon mass per unit area, 7168 g soil m^{-2}, and mean organic horizon %N (g N per g soil) from both sides, we found that the organic horizon N pool was 774 and 996 kg N ha^{-1} on the west and east, respectively. Human population in Front Range counties has increased exponentially since 1900 (US Census Bureau 1997). Assuming, after Galloway and others (1994) and Vitousek and others (1997), that increases in N deposition would parallel increases in population, we fit an exponential curve representing increases in N deposition to the population growth curve, with N deposition reaching 4.7 kg N ha^{-1} y^{-1} in 1995. We assumed that 95% of atmospheric N inputs end up in the organic horizon N pool (Baron and others 1994; Nadelhoffer and others 1999). From 1900 to the present, an estimated 162 kg N ha^{-1} has accumulated in east-side forest soils. This accounts for 73% of the difference in organic horizon N pools between east and west sites. Emmett and others (1998) and Lovett and Rueth (1999) performed similar calculations and concluded that N deposition inputs could account

Table 4. Summary of Mineral Soil Horizon Characteristics

Analysis	East Average	East Range	West Average	West Range	*P* Value
N (%)	0.35 (0.2)	0.12–1.24	0.24 (0.2)	0.03–1.74	0.08
C (%)	7.29 (4.5)	1.89–25.9	6.65 (6.6)	0.94–39.4	0.68
C:N	21.2 (4.9)	13.3–41.7	27.2 (7.8)	3.06–51.2	0.01
pH	4.76 (0.2)	4.42–5.19	5.02 (0.5)	4.10–6.41	0.21
OM	0.15 (0.1)	0.05–0.47	0.13 (0.1)	0.04–0.57	0.55
Sand (%)	40.3 (12)	21.2–75.5	48.3 (14)	20.2–76.7	0.11
Silt (%)	32.8 (8.4)	11.4–50.0	29.7 (9.6)	7.40–48.2	0.31
Clay (%)	26.9 (4.9)	13.0–44.0	22.0 (6.4)	12.4–42.8	0.03
Ca (mg/kg)	1281 (707)	300–3600	1597 (1221)	91–5000	0.46
Mg (mg/kg)	220 (77)	98–470	237 (151)	48–760	0.83
K (mg/kg)	251 (94)	110–490	274 (143)	59–670	0.59
Na (mg/kg)	81 (20)	33–130	82 (29)	42–160	0.87
P (mg/kg)	8.2 (5.5)	3.1–37	6.2 (4.5)	0.68–29	0.13

Mean and one standard deviation (SD) are given in parentheses; range is minimum and maximum values.
Nitrogen and carbon are percentages of oven-dry weight.
OM is the fraction of organic matter.
Sample n = 90 for east and west sites.
Degrees of freedom are 10 for all analyses.

for changes in soil N. This is obviously a simplification, but our estimate shows that a significant portion of the difference in organic horizon N pools could be attributed to the increases in N deposition inputs.

Discussion

Forest ecosystems differ in their ability to respond to increases in N deposition and the rate of their response (Aber and others 1998). We still do not completely understand what the factors are that control these differences. Other research has suggested that land-use history, the size of the soil N pool, and the length of the growing season are important factors in determining how fast forest stands respond to increased atmospheric N inputs (Fenn and others 1998). These factors play an important role in determining the balance between N availability and demand. We believe that the east-side Colorado Front Range forests are now reaching a point where subtle changes in the N balance are beginning to be identified.

East sites had greater soil and foliar N and lower C:N ratios than west sites. In addition, we found significantly greater foliar N:Mg ratios at the east sites. Other studies have yielded similar results in response to elevated N deposition (Aber and others 1998; Fenn and others 1998).

There are many factors that can influence N cycling, N pools, and foliar chemistry, including species composition and age, elevation, aspect, parent material, site history, climate, soil texture and N deposition (Mitchell and others 1996; Waring and Running 1998). We have therefore considered the possibility that these factors confounded our interpretations.

Elevation, aspect, parent material, and site history were controlled during site selection; therefore, these are unlikely causes for the observed differences. Stand characteristic data indicate that we effectively controlled stand age and species composition (Table 2). Nor do the soil properties we measured point to any obvious differences between the east and west sites (Table 4).

West sites are drier than east sites (86 versus 104 cm precipitation per year), but their temperatures are similar (Table 1). Seventy-two percent (13 cm) of the difference in moisture occurs during the winter months, when precipitation falls in the form of snow. The greatest effect of the snowfall is likely to be a prolongation of the period in spring when soils are saturated; however, this should not affect nutrient cycling rates because soil moisture tends to remain high through July at all sites. Could a difference of 5 cm in precipitation during the growing season influence biogeochemical processes? In mesic forests like the ones we studied, growth is correlated with summer temperatures and not with precipitation, as in xeric forests (Peet 1989; Villalba and others 1994). A simulation of a subalpine spruce–fir forest under conditions of climate change

Table 5. Summary of Organic Horizon Characteristics by Site

Site Name (Abbreviation)	Side	Mass (kg m^{-2})	Total N(g N m^{-2})	N (%)	C (%)	C:N	Lignin (%)	Lignin:N	Mineralization Rate (μg N g^{-1} d^{-1})	Nitrification Rate (μg N g^{-1} d^{-1})	Resin Bag NO_3^- (mg N y^{-1})	Resin Bag NH_4^+ (mg N y^{-1})
Boreas Pass (BR)	W	8.4 (1.4)	76 (16)	0.91 (0.2)	30.0 (5.5)	33.1 (2.5)	26.4 (5.1)	29.1 (2.6)	0.68 (1.2)	0.24 (0.7)	0.06 (0.05)	0.18 (0.3)
Fool Creek (FC)	W	6.7 (1.2)	61 (17)	0.89 (0.2)	32.1 (4.8)	36.3 (3.7)	28.0 (5.6)	31.5 (3.6)	0.23 (0.4)	0 (0)	0.05 (0.05)	0.17 (0.2)
Byers Creek (BC)	W	6.9 (1.6)	73 (20)	1.00 (0.3)	30.8 (9.1)	28.7 (8.0)	28.0 (3.4)	26.3 (2.9)	0.94 (1.5)	0 (0)	0.13 (0.1)	0.25 (0.2)
West Rollins (WR)	W	9.7 (2.4)	94 (21)	1.00 (0.2)	35.0 (7.2)	35.5 (7.7)	32.2 (7.5)	33.0 (9.5)	0.91 (0.9)	0.10 (0.2)	0.11 (0.1)	0.13 (0.1)
West Arapaho (WA)	W	4.8 (1.2)	57 (13)	1.22 (0.2)	35.5 (4.8)	29.6 (3.5)	30.0 (5.6)	24.9 (3.5)	0.28 (0.4)	0 (0)	0.05 (0.06)	0.19 (0.1)
Granite Falls (GF)	W	5.6 (1.8)	75 (21)	1.36 (0.2)	39.6 (3.1)	29.4 (2.8)	33.2 (3.7)	24.7 (3.0)	1.09 (1.0)	0.02 (0.01)	0.01 (0.02)	0.10 (0.1)
Long Lake (LL)	E	7.9 (2.0)	99 (23)	1.28 (0.1)	34.0 (5.6)	26.5 (2.1)	30.8 (5.2)	24.1 (2.8)	2.81 (1.5)	0.37 (0.6)	0.36 (0.4)	0.18 (0.3)
East Rollins (ER)	E	7.1 (1.6)	93 (21)	1.32 (0.2)	34.2 (4.5)	25.9 (1.4)	28.5 (3.7)	21.7 (1.4)	2.91 (1.5)	0 (0)	0.17 (0.3)	0.47 (0.4)
Berthoud Pass (BP)	E	8.3 (2.4)	107 (33)	1.29 (0.1)	36.4 (3.6)	28.3 (2.2)	31.3 (4.2)	24.3 (2.9)	1.80 (2.1)	0.09 (0.1)	0.28 (0.3)	0.24 (0.3)
Loch Vale (LV)	E	7.7 (1.4)	117 (23)	1.40 (0.4)	33.6 (10.5)	22.4 (6.6)	31.2 (5.0)	20.9 (3.2)	4.86 (4.7)	1.98 (2.7)	1.39 (1.7)	0.88 (1.0)
Marmot Point (MP)	E	7.1 (1.9)	98 (24)	1.29 (0.4)	34.3 (9.7)	24.8 (6.9)	30.9 (2.9)	22.4 (1.9)	3.84 (1.6)	0.27 (0.3)	0.22 (0.3)	0.21 (0.5)
Mills Lake (ML)	E	5.9 (1.9)	91 (30)	1.56 (0.2)	37.5 (4.2)	24.2 (3.0)	30.6 (3.8)	19.8 (3.1)	4.31 (2.4)	0.72 (1.8)	3.11 (12)	0.19 (0.3)
East Side Average	—	7.3 (2.0)	100 (27)	1.39 (0.2)	38.8 (4.8)	25.9 (2.7)	30.5 (4.2)	22.2 (3.1)	3.42 (2.7)	0.57 (1.5)	1.03 (5.5)	0.37 (0.6)
West Side Average	—	7.0 (2.3)	73 (22)	1.08 (0.2)	34.2 (5.9)	32.4 (5.0)	29.6 (5.7)	28.3 (5.7)	0.69 (1.0)	0.06 (0.3)	0.07 (0.1)	0.17 (0.2)
P Value	—	0.70	0.002	0.006	0.31	0.001	0.47	0.004	0.0002	0.12	0.13	0.13

Mean and one standard deviation (SD) are given in parentheses.
Side indicates either east (E) or west (W) of the Continental Divide.
Mass is the weight of organic horizon soil per square meter. Total N is the organic horizon N pool calculated using %N and the mass of the organic horizon.
Nitrogen, carbon, and lignin are percentages of oven-dry weight.
Mineralization and nitrification rates are net potential rates.
Soil ion exchange resin bags were used to estimate yearly leaching losses.
Sample n = 15 per site.
Degrees of freedom are 10 for all analyses.

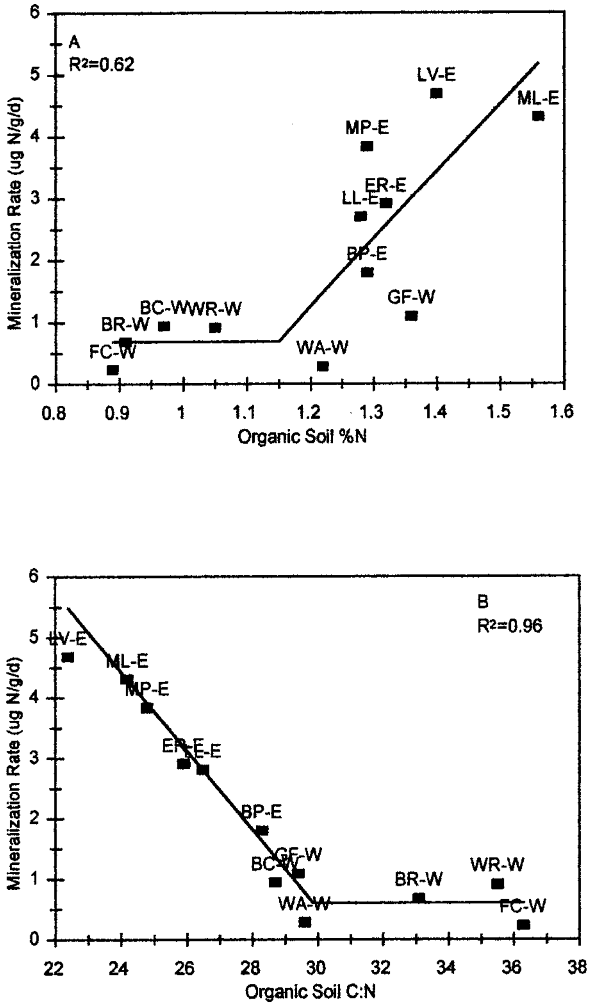

Figure 3. Relationship between organic horizon potential net mineralization rates and **A** %N and **B** C:N ratios. Point labels correspond to the site abbreviations in Figure 1 followed either by E or W to indicate whether the site is located east or west of the Continental Divide.

also suggested that precipitation does not act as a major control on ecosystem processes (Baron and others 2000a). When annual and seasonal precipitation and temperature were varied by ±10% and ±2°C, respectively, forest productivity, evapotranspiration, and soil moisture were unresponsive to changes in precipitation but sensitive to changes in temperature. The growth rates were comparable at the east and west sites for both the cool–wet and warm–dry climatic periods that we examined. If differences in the moisture regime were driving the observed biogeochemical differences between the east and west sites, we would expect to see increased growth rates at the west sites during the cool–wet period from 1900 to 1929 (Table 2). Because we did not, we conclude that the slight differences in climate between the east and west sites could not have resulted in growth rate differences between the two sides.

East-side soil had a significantly greater percentage of clay, with an absolute difference of 4.9% (Table 4). Soil texture was highly variable, and the range of values was similar for both sides. Differences in soil clay content could influence biogeochemistry through two primary mechanisms—stand productivity and soil organic matter dynamics (Burke 1989; Aber and Melillo 1991; Parton and others 1994). Because there were no differences in tree growth rates and organic matter pools between the east and west sites, we conclude that the estimated difference in soil clay content is not large enough to influence N dynamics (Tables 2, 4, and 5).

Mineral soil %N is marginally greater at east sites, with an average difference of 0.11%. Organic matter stabilization increases and turnover rate decreases with greater clay content, thereby facilitating C and N accumulation in soil (Sorenson 1981; Paul 1984; Schimel and others 1985; Parton and others 1987). During soil development since the last glaciation (approximately 7000 year ago) (Madole 1976), greater soil clay content at the east sites most likely resulted in slightly higher mineral soil N. However, greater mineral soil N does not necessarily equate to higher N availability because clay-stabilized organic matter has low turnover rates.

Gundersen and others (1998) examined data from five European sites that span an N-deposition gradient of 13–59 kg ha^{-1} y^{-1} and found no relationship between either the mineral soil N pool size or the C:N ratio and forest N status, vegetation variables, or forest floor characteristics. Their results suggest that mineral soil is not a large sink for atmospheric N deposition and that the mineral soil N pool does not drive biogeochemical processes associated with changes in N inputs. They also found, as we did, that the mineral soil N pool was correlated with clay content. Therefore, we assume that differences in mineral soil N did not result in greater N availability at the east sites prior to the elevation of atmospheric N inputs. The influence of increased N deposition on soil properties is expected to be strongest in the organic horizon (Gundersen and others 1998; Nadelhoffer and others 1999). We found that 73% of the difference between east and west organic matter N pools could be accounted for by N deposition.

McNulty and others (1991) conducted a study similar to ours examining spruce–fir N dynamics across an N-deposition gradient in the northeastern United States. They found a linear increase in net nitrification rates when forest floor %N increased above 1.4%. We observed a similar relation between potential net mineralization rates and organic horizon %N (Figure 3A). As %N increased above 1.2%, net mineralization rates increased linearly. No relation was seen between potential net nitrification rates and soil %N because net nitrification rates were low at most sites. Higher net nitrification rates were observed at the two sites with the lowest soil C:N ratios. Loch Vale (LV) and Mills Lake (ML) had C:N ratios of 22.4 and 24.2 and nitrification rates of 1.98 and 0.72 $\mu g\ g^{-1}\ d^{-1}$, respectively (Table 5). Other investigators have found a nitrification threshold related to soil C:N ratios where nitrification is limited in soils with a C:N ratio greater than 25 or 24 (Gundersen and Rasmussen 1990; Emmett and others 1998; Lovett and Rueth 1999). The low nitrification rates observed at most of the sites in this study could be explained by soil C:N ratios above this threshold.

Our data suggest a positive feedback from atmospheric N additions where increased soil N pools lead to increased soil N mineralization rates, which increases plant-available N (Tietema and others 1995). The organic horizon N pool is the primary sink for incoming N (Fenn and others 1998; Nadelhoffer and others 1999). We found an increase in organic horizon %N and total N and a decrease in C:N and lignin:N ratios at the east sites as compared to the west ones. This increase in soil N can lead to the more rapid N mineralization rates (Aber and others 1998) that we observed at the east sites relative to the west ones. Higher N mineralization rates can result in greater plant N availability. Foliar %N was greater at east than at west sites. Increased foliar %N caused decreased foliar C:N ratios. Changes in foliar C and N can generate a positive feedback, further decreasing soil C:N and lignin:N ratios through foliar litter inputs (Melillo and others 1982). If soil C:N ratios continue to decline, nitrification rates may increase (Emmett and others 1998; Gundersen and others 1998). The two sites with the lowest soil C:N ratios had higher potential net nitrification rates and estimated NO_3^- leaching losses (Table 5).

Conclusions

Increased N deposition results in increased foliar %N and N:Mg ratios, decreased foliar and soil C:N ratios, and changes in N mineralization rates (Aber and others 1998; Fenn and others 1998; Gundersen and others 1998; Vitousek and others 1997). Our six east sites displayed all of these characteristics, which are indicative of greater N availability. Other gradient studies have shown vegetation and soil responses to increased N inputs; however, the range of deposition rates in those studies was greater than in our study (McNulty and others 1991; Tietema and Beier 1995; Lovett and Rueth 1999). Our results suggest that even relatively small increases in N-deposition inputs may cause measurable changes in the biogeochemical processes of forests.

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References

Aber J, McDowell W, Nadelhoffer K, Magill A, Berntson G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. BioScience 48:921–34.

Aber JD, Melillo JM. 1991. Terrestrial ecosystems. Saunders College Publishing: Philadelpha.

Baron JS, Denning AS. 1993. The influence of mountain meteorology on precipitation chemistry at low and high elevations of the Colorado Front Range, USA. Atmos Environ 27A:2337–49.

Baron JS, Hartman MD, Band LE, Lammers RB. 2000a. Sensitivity of a high-elevation Rocky Mountain watershed to altered climate and CO_2. Water Resources Res 36:89–99.

Baron JS, Ojima DS, Holland EA, Parton WJ. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: implications for aquatic systems. Biogeochemistry 27: 61–82.

Baron JS, Rueth HM, Wolfe AM, Nydick KR, Allstott EJ, Minear T, Moraska B. 2000b. Ecosystem responses to nitrogen deposition in the Colorado Front Range. Ecosystems 3:352–68.

Binkley D, Hart S. 1989. The components of nitrogen availability assessments in forest soils. Adv Soil Sci 10:57–112.

Bossert JE. 1990. Regional-scale flows in complex terrain: an observational and numerical investigation [dissertation]. Fort Collins (CO): Department of Atmospheric Science, Colorado State University. 257.

Burke IC. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. Ecology 70:1115–1126.

Campbell DH, Baron JS, Tonnessen KA, Brooks PD, Schuster PF. 2000. Controls on nitrogen flux in alpine/subalpine watersheds of Colorado. Water Resources Res 36:37–47.

Emmett BA, Boxman D, Bredemeier M, Gundersen P, Kjønass OJ, Moldan F, Schleppi P, Tietema A, Wright RF. 1998. Predicting the effects of atmospheric nitrogen deposition on conifer stands: evidence from the NITREX ecosystem-scale experiments. Ecosystems 1:352–60.

Fenn ME, Poth MA, Aber JD, Baron JS, Bormann BT, Johnson DW, Lemly AD, McNulty SG, Ryan DF, Stottlemyer R. 1998.

Nitrogen excess in North America ecosystems: a review of predisposing factors, geographic extent, ecosystem responses, and management strategies. Ecol Appl 8:706–33.

Fernandez IJ, Lawrence GB, Richards KJ. 1990. Characteristics of foliar chemistry in a commercial spruce–fir stand of northern New England, USA. Plant Soil 125:288–92.

Galloway JN, Levy H II, Kasibhatla PS. 1994. Year 2020: Consequences of population growth and development on deposition of oxidized nitrogen. Ambio 23:120–3.

Goering HK, Van Soest PJ. 1970. A system for forage fiber analysis including equipment, reagent, methods and some analysis application. USDA Agricultural Research Series handbook no. 379.

Gundersen P, Emmett BA, Kjønass OJ, Koopmans CJ, Tietema A. 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. For Ecol Manage 101:37–55.

Gundersen P, Rasmussen L. 1990. Nitrification in forest soil: effects of nitrogen deposition on soil acidification and aluminum release. Rev Environ Contamination Toxicol 113:1–45.

Haase DL, Rose R. 1995. Vector analysis and its use for interpreting plant nutrient shifts in response to silvicultural treatments. For Sci 41:54–66.

Heuer K, Tonnessen KA, Ingersoll GP. 2000. Comparison of precipitation chemistry in the Central Rocky Mountains, Colorado, USA. Atmos Environ 34:1723–37.

Kiefer JW, Fenn ME. 1997. Using vector analysis to assess nitrogen status of ponderosa and Jeffrey pine along deposition gradients in forests of southern California. For Ecol Manage 94:47–59.

Klute A, editor. 1986. Methods of soil analysis; Pt 1. Physical and mineralogical methods. 2nd ed. Madison (WI): American Society of Agronomy, Soil Science Society of America.

Langford AO, Fehsenfeld FC. 1992. Natural vegetation as a source or sink for atmospheric ammonia: a case study. Science 225:581–3.

Lovering TS, Goddard EN. 1950. Geology and ore deposits of the Front Range, Colorado. USGS professional paper no. 223. Denver (CO): US Geological Survey.

Lovett GM, Rueth HM. 1999. Soil nitrogen transformations in beech and maple stands along a nitrogen deposition gradient. Ecol Appl 9:1330–44.

McNulty SG, Aber JD, Boone RD. 1991. Spatial changes in forest floor and foliar chemistry of spruce–fir forests across New England. Biogeochemistry 14:13–29.

Madole RF. 1976. Glacial geology of the Front Range, Colorado. In: Mahaney WC, editor. Quaternary stratigraphy of North America. Stroudsburg (PA): Dowden, Hutchinson & Ross. p297–398.

Melillo JM, Aber JD, Muratore JF. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–6.

Mitchell MJ, Driscoll CT, Kahl JS, Likens GE, Murdock PS, Pardo LH. 1996. Climatic control of nitrate loss from forested watersheds in the northeast United States. Environ Sci Technol 30:2609–12.

Nadelhoffer KJ, Downs MR, Fry B. 1999. Sinks for ^{15}N-enriched additions to an oak forest and a red pine plantation. Ecol Appl 9:72–86.

[NADP/NTN] National Atmospheric Deposition Program (NRSP-3)/National Trends Network. 1999. Illinois state water survey. Champaign (IL): NADP Program Office.

Natural Resources Conservation Service, National Water and Climate Center. 1999. Portland (OR): NRCS Program Office.

Page AL, editor. 1982. Methods of soil analysis; Pt 2. Chemical and microbiological properties. 2nd ed. Madison (WI): American Society of Agronomy, Soil Science Society of America.

Parrish DD, Norton RB, Bollinger MJ, Liu SC, Murphy PC, Albritton DL, Fehsenfeld FC. 1986. Measurements of HNO_3 and NO_3^- particulates at a rural site in the Colorado Mountains. J Geophys Res 91:5379–93.

Parrish DD, Hahn CH, Fahey DF, Williams EJ, Bollinger MJ, Hübler G, Buhr MP, Murphy PC, Trainer M, Hsie EY, and others. 1990. Systematic variations in the concentration of NO_x (NO plus NO_2) at Niwot Ridge, Colorado. J Geophys Res 95:1817–36.

Parton WJ, Ojima DS, Cole CV, Schimel DS. 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. In: Quantitative modeling of soil forming processes. SSSA special publication no. 39. Bryant RB, Arnold RW 137–167.

Parton WJ, Schimel DS, Cole CV, Ojima DS. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci Soc Am J 51:1173–9.

Paul EA. 1984. Dynamics of organic matter in soils. Plant Soil 76:275–85.

Peet RK. 1989. Forests of the Rocky Mountains. In: Barbour MG, Billings WD, editors. North American Terrestrial vegetation. New York: Cambridge University Press. p 63–101.

Peet RK. 1981. Forest vegetation of the Colorado Front Range. Vegetatio 45:3–75.

Phipps RL. 1985. Collecting, preparing, cross-dating, and measuring tree increment cores. US Geological Survey water-resources investigations report 85–4148, no. 261855.

SAS. 1989. SAS/STAT user's guide; version 6. 4th ed. Cary (NC): SAS Institute.

Schimel DS, Coleman DC, Horton KA. 1985. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma 36:201–14

Self JR, Rodriguez JB. 1998. Laboratory manual for SC-564: Soil and plant chemical analysis. Fort Collins (CO): Soil, Water, and Plant Testing Laboratory, Department of Soil and Crop Sciences, Colorado State University.

Sievering H, Braus J, Caine J. 1989. Dry deposition of nitrate and sulfate to coniferous canopies in the Rocky Mountains. In: Olson RK, Lefohn AS, editors. Transactions effects of air pollution on western forests. Pittsburgh (PA): Air and Waste Management Association. p 171–176.

Sievering H, Rusch D, Marquez L. 1996. Nitric acid, particulate nitrate and ammonium in the continental free troposphere: nitrogen deposition to an alpine tundra ecosystem. Atmos Environ 30:2527–37.

Sorensen LH. 1981. Carbon–nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. Soil Biol Biochem 13:313–21.

Stokes MA, Smiley TL. 1968. An introduction to tree-ring dating. Chicago: University Press.

Stottlemyer R, Troendle CA. 1992. Nutrient concentration pattern in streams draining alpine and subalpine catchments. Fraser Experimental Forest, Colorado. J Hydrol 140:179–208.

Stottlemyer R, Troendle CA, Markowitz D. 1997. Changes in snowpack, soil water, and stream water chemistry with elevation during 1990, Fraser Experimental Forest, Colorado. J Hydrol 195:114–36.

Tietema A, Beier C. 1995. A correlative evaluation of nitrogen cycling in the forest ecosystems of the EC projects NITREX and EXMAN. For Ecol Manage 71:143–51.

Tietema A, Wright RF, Blanch K, Boxman AW, Bredemeier M, Emmett BA, Gundersen P, Hultberg H, Kjønass OJ, Moldan F, and others. 1995. NITREX: the timing of response of coniferous forest ecosystems to experimentally-changed nitrogen deposition. Water Air Soil Pollut 85:1623–8.

Timmer VR, Stone EL. 1978. Comparative foliar analysis of young balsam fir fertilization with nitrogen, phosphorus, potassium, and lime. Soil Sci Soc Am J 42:125–30.

US Census Bureau. 1997. Population distribution and population estimates branches. Washington (DC): United State Department of Commerce Available on the Internet: http://www.census.gov/population/www/estimates/popest.html.

Veblen TT, Kitzberger T, Donnegan J. 2000. Climatic and human influences on fire regimes in ponderosa pine forest in the Colorado Front Range. Ecol Appl 10:1178–95.

Villalba R, Veblen TT, Ogden J. 1994. Climate influences on the growth of subalpine trees in the Colorado Front Range. Ecology 75:1450–62.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle sources and consequences. Ecol Appl 7:737–50.

Waring RH, Running SW. 1998. Forest ecosystems analysis at multiple scales. Academic Press.

Williams MW, Bardsley T, Rikkers M. 1998. Overestimation of snow depth and inorganic nitrogen wetfall using NADP data, Niwot Ridge, Colorado. Atmos Environ 32:3827–33.

Williams MW, Tonnessen KA. 2000. Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA. Ecol Appl 10:1648–65.